Oecologia (1998) 114:461-470

Chloe S. Schauble - Gordon C. Grigg

Thermal ecology of the Australian agamid *Pogona barbata*

Received: 28 April 1997 / Accepted: 29 December 1997

Abstract
This study compares the thermal ecology of male bearded dragon lizards *(Pogona barbata)* from south-east Queensland across two seasons: summer (1994-1995) and autumn (1995). Seasonal patterns of body temperature (T_b) were explored in terms of changes in the physical properties of the thermal environment and thermoregulatory effort. To quantify thermoregulatory effort, we compared behavioral and physiological variables recorded for observed lizards with those estimated for a thermoconforming lizard. The study lizards' field T_bs varied seasonally (summer: grand daily mean (GDM) 34.6±0.6°C, autumn: GDM 27.5±0.3°C) as did maximum and minimum available operative temperatures (summer: GDM T_{max} 42.1±1.7°C, T_{min} 32.2±1.0°C, autumn: GDM T_{max} 31.7±1.2°C, T_{min} 26.4±0.5°C). Interestingly, the range of temperatures that lizards selected in a gradient (selected range) did not change seasonally. However, *P. barbata* thermoregulated more extensively and more accurately in summer than in autumn; lizards generally displayed behaviors affecting heat load nonrandomly in summer and randomly in autumn, leading to the GDM of the mean deviations of lizards' field T_bs from their selected ranges being only 2.1±0.5°C in summer, compared to 4.4±0.5°C in autumn. This seasonal difference was not a consequence of different heat availability in the two seasons, because the seasonally available ranges of operative temperatures rarely precluded lizards from attaining field T_bs within their selected range, should that have been the goal. Rather, thermal microhabitat distribution and social behavior appear to have had an important influence on seasonal levels of thermoregulatory effort.
C.S. Schauble. G.C. Grigg.

Department of Zoology, The University of Queensland, Brisbane, Queensland 4072, Australia

Key words *Pogona barbata* - Thermoregulation Selected range - Radiotelemetry - Operative temperatures

Introduction

In 1963 George Bartholomew and Vance Tucker found that specimens of *Pogona barbata* (formerly *Amphibolurus barbatus)* exposed to step-function changes in temperature under laboratory conditions heated up faster than they cooled down (Bartholomew and Tucker 1963). Little was known about the thermal relations of *P. barbata* in natural circumstances but, from anecdotal information and a study by Lee and Badham (1963), *P. barbata* was assumed to thermoregulate behaviorally during the daily activity period (see also Brattstrom 1971). Thus, the adjustment in whole-body thermal conductance was interpreted in terms of its potential benefit in the regulation of body temperature (T_b) under field conditions, allowing a reptile to gain heat rapidly by basking, then lose it slowly, thus minimizing the time needed for thermoregulation. This phenomenon was described in other species also, with a similar interpretation, and has come to be regarded as having wide application among reptiles (Bartholomew 1982).

The field of thermal ecology has changed greatly since 1963, however, and the study of Lee and Badham (1963) would no longer be considered adequate proof of field thermoregulation. In the light of the observations of Bartholomew and Tucker (1963), and the widespread interest they generated, it is surprising that no-one has looked further at thermoregulation in *P. barbata* using modern protocols. (Neither has anyone tried to ascertain whether or not the ability to modify whole-body thermal conductance is functionally significant in these or any other reptiles in a field situation). Our study examines the thermal ecology of *P. barbata* in a subtropical habitat over two seasons, summer and autumn, focusing in particular on determining the extent of its thermoregulation.

As shown by the studies of Christian et al. (1983), Christian and Tracy (1985) and van Damme et al. (1987), important information can be gained by looking at a reptile's thermal ecology over more than one season. Seasonal T_b changes might reflect shifts in physiological factors such as the animals' selected ranges (acclimatization) (Christian et al. 1983; Seebacher 1993), or intrinsic hormonal rhythms (Garrick 1974, 1979; Shine 1980; van Damme et al. 1987). Also, changes in ecological factors like food supply (Christian et al. 1983; Shine and Lambeck 1990; Christian and Bedford 1995) and the availability of particular thermal habitats (Peterson 1987; Grant 1990) may cause seasonal

changes in T_b. The above factors are not mutually exclusive and are likely to act in combination with one another.

Strict thermoconformity, as in *Anolis polylepis* (Hertz 1974), and strict thermoregulation, as in *Dipsosaurus dorsalis* (DeWitt 1967), can be thought of as the opposite ends of a continuum of thermoregulatory patterns (Huey and Slatkin 1976; Hertz et al. 1993). Although many reptiles may be primarily thermoconformers or thermoregulators, some species appear to exhibit both thermoconformity and thermoregulation, depending on the situation (Huey 1974; Huey and Webster 1976; Shine and Lambeck 1990; Kingsbury 1994). Where does *P. barbata* fit into this spectrum? Answering this question relies upon being able to discriminate effectively between various degrees of thermoregulatory activity.

The last 5-10 years have seen significant advances in both the theoretical and practical frameworks for studies of thermal ecology (e.g., Hertz et al. 1993; Diaz 1994; Christian and Bedford 1995; Bauwens et al. 1996; Christian and Weavers 1996). It is no longer sufficient to simply compare T_bs to ambient temperatures when trying to understand an ectotherm's response to its thermal environment. To detect evidence for thermoregulation, or expose its absence, body temperatures need to be compared with achievable operative temperatures (Bakken 1992). However, a comprehensive evaluation of thermoregulation also requires direct observations of behaviors which affect heat load (Hertz et al. 1993). Past studies have tended to concentrate on either the behavioral aspects of thermoregulation, or on comparing operative temperatures with body temperatures (although Diaz 1994; Bauwens et al. 1996; Christian and Weavers 1996 provide notable exceptions). A more satisfactory approach is to combine the two viewpoints by recording behavior and temperature data simultaneously.

Our study sets out to answer three questions. Do *P. barbata* thermoregulate in the field? Are there seasonal changes in the field T_bs and thermoregulatory activity of *P. barbata* in south-east Queensland? What are the major factors responsible for any similarities or differences between the seasonal field T_bs of *P. barbata?* The two initial questions can be answered in an absolute sense.

First, if it can be shown that lizards do not behave randomly in terms of factors affecting heat load, and that their T_bs differ from those that a thermoconforming lizard would display, this would provide strong evidence that they are thermoregulating. Second, field T_bs are easily compared between seasons and we might expect autumn body temperatures in subtropical Queensland to be lower than those recorded in summer. Also, recording variables such as operative temperatures and the level of thermally related behaviors allows us to compare the extent of thermoregulatory activity in each season. Concerning the third question, we use quantitative comparisons to eliminate factors which appear unlikely to be responsible for any observed changes in field T_bs.

Materials and methods

Identifying thermoregulation

We modified the comprehensive protocol of Hertz et al. (1993) for detecting thermoregulation. Our version consists of five steps:

1. Measure field T_bs of free-ranging lizards by radiotelemetry.
2. Compare the expression of behavior patterns affecting heat load by lizards in the field with that estimated for a thermoconforming lizard (a "random lizard"). (In the absence of data describing the way foraging and social requirements influence lizard movement patterns, we must assume that a thermoconformer both behaves and travels through its habitat randomly).
3. Using a physical model moved at random, measure the distribution of T_bs that a random lizard would experience in that habitat.
4. Using a thermal gradient, estimate the physiological "target range" of T_bs that lizards presumably attempt to achieve when both abiotic and biotic circumstances and requirements do not constrain T_b selection.
5. Compare the field T_bs, and the values of an index of thermoregulatory accuracy recorded for the study lizards with those estimated for a random lizard.

Study animals and telemetry

Two field sites were chosen near Laidley in south-east Queensland, a small area at Mt. Berryman (27°42'S, 152°20'E), and the Laidley Golf Course (27°38'S, 152°24'E, approximately 12 km north-north-east of the Mt. Berryman site). Both sites have a subtropical climate and have both open forest and grassy areas. *P. barbata* are diurnal and semiarboreal agamid lizards (Griffiths 1987; Cogger 1992). According to Lee and Badham (1963) the activity period for these lizards in south-east Queensland runs from September to May.

Temperature-sensitive two-stage radio transmitters (Sirtrach. NZ) with external loop antennas were inserted surgically into the peritoneal cavities of *P. barbata*. Only male lizards were used because the small size of females made most of them unsuitable for transmitter implantation. Lizards were anaesthetized via intubation with gaseous halothane and surgery was carried out using aseptic techniques similar to those used by Manning and Grigg (1997). All experimental animals weighed more than 400 g (424-583 g) and transmitters always represented less than 5% of body weight. We calibrated the transmitters in a water bath against a certified mercury thermometer (±0.1°C) before implantation. We measured the field body temperatures of the lizards, represented by intervals between transmitted pulses, using a digital processor (Telonics) connected to a radio receiver (Telonics) and an H-frame antenna.

We observed four lizards intensively for two to four days each in summer (December-January 1994-1995) and then again in autumn (April 1995). Unfortunately, only two of the summer lizards survived to autumn. Two replacement lizards were implanted with transmitters, then released into the field at least 1 month before the autumn sampling commenced.

Selected T_b range

Despite the limitations inherent in placing animals in artificial environments, the range of T_bs selected by an animal in a laboratory thermal gradient (the *selected range)* is usually assumed to be an estimation of its physiological "target range" (Crawford 1980; van Damme et al. 1989; Christian and Bedford 1995). The target range is that range of T_bs over which the combined performance of all physiological processes is close to maximal when restrictions on T_b selection are absent (Huey 1982; Stevenson et al. 1985). Presumably lizards that are thermoregulating effectively will maintain field T_bs which are typically within the target range (Licht et al. 1966; Peterson 1987; Hertz et al. 1993). Taken a step further, for our purposes, their T_bs should be within their own selected range more often than are those of a lizard which thermoconforms (the random lizard).

We determined the selected ranges for each experimental lizard in a thermal gradient immediately after the completion of each season's field observations. Selected T_b ranges were taken as the central 50% (Hertz et al. 1993; Christian and Weavers 1996) of the T_bs recorded in the gradient between 0905 and 1600 hours. This was done for both seasons and for each experimental lizard. The thermal gradient was in a constant temperature room set at 23°C. Radiant heat was supplied by 75-W opaque bulbs at one end of the gradient. These provided the only artificial light source. Air temperatures along the gradient ranged from 23°C to at least 45°C. Photoperiod (and hence the time for which heat was available) was set according to local sunrise and sunset.

During sampling times we recorded the signal from each lizard's transmitter automatically using a recording-receiver system designed by Grigg et al. (1992). To avoid any possible effects of acclimation to laboratory conditions (van Damme et al. 1987; Slip and Shine 1988) lizards were transferred directly from the field to the gradient. Water was supplied ad libitum but food was withheld. Lizards remained in the gradient for three to five days. The upper and lower end points of the selected range were determined each day for each lizard. A mean selected range was then calculated for each lizard. For the analyses in this study, the field T_bs experienced by each lizard (and T_{min} and T_{max}) are compared only to that lizard's own mean selected range (for the appropriate season).

Field observations of lizards

Two behavioral mechanisms known to have significant effects on reptilian heat loads are the selection of microhabitats and choice of the body's angle of orientation to the sun (reviewed by Heatwole and Taylor 1987; Huey 1991; see Adolf 1990; Diaz 1992 for specific examples). As both microhabitat selection and body orientation can exert a substantial effect on a lizard's T_b we use both of them as behavioral indicators of thermoregulatory effort.

A set of observations taken from a particular lizard for a particular day is referred to as a "lizard-day". During daily observation periods (0905-1600 hours) we recorded the following information for each lizard at 5-min intervals:

I. Body temperature (°C) measured by *radiotelemetry.*

2. *Orientation of lizard to the sun* - back, side, or chest. "Back" was scored if the tail end of the lizard's head-tail axis was pointing towards the sun and parallel with its path. If the lizard had its head or chest in the direction the rays of the sun were coming from, we recorded "chest". Finally, when the sun's path was at right angles to the lizard's head-tail axis, the orientation "side" was scored. For intermediate angles we scored the closest orientation.

3. *The percentage of the lizards' surface area that was exposed to solar radiation (%sun)* - the percent *of* the total surface area of the body that would be exposed to sunshine if the sky was clear. This variable could be estimated accurately as clouds passed overhead quickly. For statistical analyses the values of %sun were divided into three major sun exposure categories (Table 1).

Table 1 Categories of sun exposure. Note that, in general, values of %sun over 50 represent times when at least the entire dorsum of the lizard is exposed to direct sunshine

Exposure category	**Definition**
Shade	%Sun < 25%
Partial sun	25% <_ %Sun ? 50%
Full sun	%Sun > 50%

Estimating the microhabitat use and orientations of a thermoconforming lizard

A realistic copper lizard model (see below) was orientated and moved randomly within the habitat. This model provided an estimate of the thermal microhabitats and body orientations that would be experienced by a lizard which behaved randomly in terms of factors affecting heat load (thermoconformed). Randomized times between each relocation of the random model were generated using a square distribution in the spreadsheet program Quattro Pro (Borland). The direction and distance of moves were also randomized in this way. We constrained the interval between moves to between 5 and 100 min, based on observations of average lizard movements. Similarly, relocation distances were kept to between 0.1 and 5 m. The direction of each move was limited to one of north. north-east, east, south-east, south, south-west, west, or north-west.

Estimating the T_bs of a thermoconforming lizard

We used physical models to measure the operative temperatures (at thermal equilibrium) available to lizards at our field sites (Hertz 1992; Buttemer and Dawson 1993; Ellner and Karasov 1993). Hollow models were constructed from copper pipe and sheeting. The proportional size and surface area of each body part was similar for live and model lizards. Models were painted grey. The reflectivities (measured between 400 and 1100 nm) of the lizard (light skin color phase only) over two trials were 0.17 and 0.19, while the reflectivity of the paint card was 0.17.

Temperature sensors incorporating miniature bead thermistors (RS Components Australia, Part 151-142) were installed in the models. The sensor tips were positioned just below the dorso-ventral midline of the body cylinders (Bakken 1992). Because thermal gradients within models can be large (Bakken 1992), we inserted a polystyrene block directly above the temperature sensor in order to reduce any possible bias in measured temperatures caused by the proximity of the sensor to the dorsal surface. The sensors were connected to a DT50 datalogger (Data Electronics Australia Pty. Ltd.) which recorded the temperature of the models every 5 min between 0905 and 1600 hours in summer and every 10 min in autumn.

We moved one of these models randomly through the habitat (see previous section), but did not measure its temperature as it was not possible to keep it connected to the datalogger. Two other models were used in the field to provide relatively instantaneous measurements of the maximum and minimum operative environmental temperatures available. The first model was used to estimate the operative temperature experienced (at thermal equilibrium) by a lizard in the full sun (T_{max}), while the second measured operative temperature in the full shade ($T_{min°}$). Unfortunately the construction of the models and physical logistics precluded the placement of models in trees at any stage. Since the lizards are semi-arboreal, this is an acknowledged drawback.

We estimated the T_bs of a lizard moving randomly (a thermoconforming "random lizard") by combining the operative temperatures measured by the copper models placed in the full sun (T_{max}) and full shade (T_{min}), with the proportion of time the randomly moved model was in each of the full sun, partial sun. and shade exposure categories. In this manner, we obtained estimates of a random lizard's body temperatures (T_bs) which we could directly compare with the field T_bs of real lizards:

T_A = (mean proportion of the daily observation period that the random model spent in full sun x T_{max})
+ (mean proportion of the daily observation period that the random model spent in full shade x

T_{min}) + {mean proportion of the daily observation period that the random model spent in partial sun x [(Tmax + T_{min})/2]}

where the values for the mean proportion of time the random model spent in each sun exposure category are specific to each season. Since T_A is based on actual random sampling of the thermal habitat, we consider that it provides a realistic index of the operative temperatures likely to be experienced by a thermoconforming lizard that moves randomly. Our calculation assumes that such a lizard is always at thermal equilibrium.

Determining the accuracy of thermoregulation

To determine how accurately lizards might be thermoregulating, we used an index based on those of Hertz et al. (1993) and Christian and Weavers (1996). This index (MD) is defined as the absolute mean deviation of body temperature from a particular animal's selected range, i.e., the difference between the observed T_b and the closest end of the selected range. Considered in isolation, the deviation of T_b from the selected range tells nothing about thermoregulation (Hertz et al. 1993), only that the animal is not free from environmental or ecological constraints. However, an indication of thermoregulatory activity is afforded by comparisons between the absolute mean deviations (MDs) of an individual lizard's field T_bs, its selected range, and the MDs of the T_bs estimated for a thermoconforming lizard (T_As) from the same range. If lizards are thermoregulating, their T_bs will deviate differently from those of a random lizard. Moreover, the more accurately lizards thermoregulate, the closer their T_bs will be to their selected ranges relative to those of the random lizard.

Statistical methods

Statistical analyses referred to in this study were performed using either Quattro Pro (Borland) or the statistical program SAS. Only P values <0.05 are considered significant. We were only able to observe a small number of lizards during this study, and the extent to which T_bs and behaviors were correlated across days is not known. Although we acknowledge the obvious problems associated with being unsure of the independence of the data, for the analyses presented in this paper we assume that each lizard-day is an independent sample (a particular lizard observed on a particular day).

Wilcoxon's signed rank and Kolmogorov-Smirnov tests were used to investigate the significance of differences between the frequency distributions of. (1) summer and autumn field T_bs, (2) summer and autumn selected ranges, and (3) field T_bs and selected ranges within each season. We transformed the data (either log or arcsine) used in parametric statistical analyses, and have used statistical tests that are fairly robust against violations of the underlying distribution assumptions. One-tailed *t*-tests (two-sample, assuming unequal variances) compared the mean proportions of time that each of the three body orientations was observed for, during the 0905 to 1600 hours observation period, with those expected from a randomly orientating lizard.

We carried out *F*-tests to ascertain whether variances between samples were approximately equal and then used one-way ANOVAs to evaluate differences (for each season) between the mean values of (1) the mean daily proportion of time spent in the full sun and shade by study lizards and by a random lizard, (2) the lizards' mean daily field T_bs and the mean daily T_bs of a random lizard (T_AS) and (3) the mean daily values of the mean deviation (MD) of lizards' field T_bs and of T_A from the individual lizards' selected ranges. In order to have equal sample sizes for use in the statistical tests, we compared the average daily mean of each variable for the four individual lizards with the daily means on four arbitrarily selected days within each season for the random lizard.

Results

Field T_bs and selected ranges

Field T_bs and the range of T_bs -selected in a thermal gradient are described in Tables 2 and 3 as grand daily means (GDMs), i.e., the grand mean of the mean daily value for each lizard. A marked seasonal change occurred in field T_bs, with the lizards' mean daily field T_bs being significantly higher in summer than in autumn. Furthermore, the mean central 50% ranges of lizards' summer field T_bs were significantly higher than the central 50% ranges for their selected ranges (Table 3, Fig. 1), indicating that they were generally not achieving their physiological "target" body temperatures. Nor were the lizards' autumn field T_bs matched to their selected ranges, though in this case field T_bs were significantly lower than the selected ranges (Table 3, Fig. 2).

There was an average rise of 1.7°C in the upper end of the average selected range across all lizards from summer to autumn (Table 3). The lower end rose 2.8°C. However, the difference between the frequency distributions of summer and autumn selected ranges was not statistically significant.

Table 2 Grand daily means (with SEs in parentheses) for maximum (T_{max}) and minimum (T_{min}) operative temperatures, the field body temperature of study lizards (T_b), and the estimated body temperature of a randomly moving (thermoconforming) lizard (T_A)

	Mean Tmax (°C) (SE)	Mean T_{min}(°C) (SE)	Mean field $\underline{T}_b$ (°C) (SE)	Mean T_A (°C) (SE)
Summer	42.1 (1.7)	32.2 (1.0)	34.6 (0.6)	39.8 (1.6)
Autumn	31.7 (1.2)	26.4 (0.5)	27.5 (0.3)	29.9 (0.9)

Table 3 Grand daily means (with SEs in parentheses) of the central 50% ranges of laboratory selected body temperatures, field body temperatures, and operative temperatures

		Upper endpoint (°C) (SE)	Lower endpoint (°C) (SE)
Summer	T_{max}	45.4 (1.8)	39.4 (2.0)
	T_{min}	33.6 (1.1)	31.0 (1.1)
	Field T_b	36.2 (0.8)	33.3 (0.6)
	T_A	42.7 (1.7)	37.4 (1.7)
	Selected range	33.1 (1.1)	29.2 (0.6)
Autumn	T_{max}	34.3 (1.3)	28.9 (1.3)
	T_{min}	27.6 (0.6)	25.3 (0.5)
	Field T_b	29.0 (0.3)	26.2 (0.4)
	T_A	31.8 (1.0)	27.7 (1.0)
	Selected range	34.8 (0.8)	32.0 (0.7)

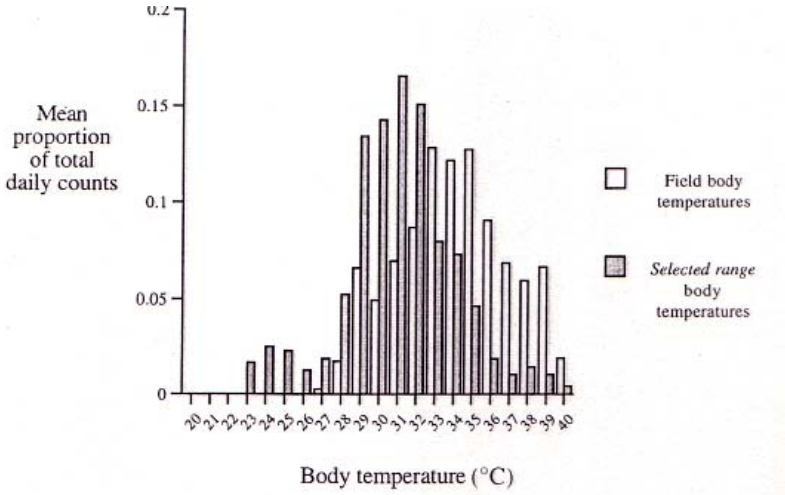

Fig. 1 Frequency distributions for summer of body temperature in the field and in a laboratory thermal gradient

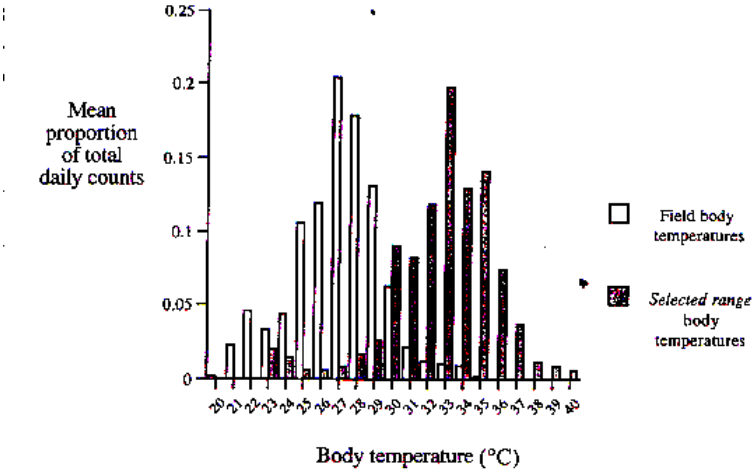

Fig. 2 Frequency distributions for autumn of body temperature in the field and in a laboratory thermal gradient

Operative temperatures available in the field

Environmental conditions on all days in both summer and autumn were generally similar. Typically, days were sunny, but cloud cover increased and decreased over short periods (e.g. within 0.5 h). The seasonal averages of mean daily T_{max} and T_{min} for both seasons are contained in Table 2. The central 50% ranges and the MD of field T_{bs}, fell between those of T_{min} and T_{max} in both summer and autumn (Tables 3 and 4). These facts suggest that, in isolation, operative temperatures did not constrain the lizards from achieving T_bs within their selected ranges (either by being too low or too high). Visual inspection of daily graphs of T_{max} and T_{min} between 0905 and 1600 hours (Fig. 3, compare also Fig. 4 for autumn), and the mean value of T_{min} (Table 2), indicates that the selected range may sometimes have been unavailable for around an hour in the middle of the day in summer. However, the operative temperatures available at the tops of large trees, where wind speed was significantly higher than on the ground (see Stevenson 1985), were probably cooler than those measured by our models. Therefore, treetops might have supplied microhabitats where T_bs within the selected range were attainable for the whole of the observation period. Indeed, on one occasion in summer a lizard remained high in a tree for a whole observation period and its T_b remained within its selected range.

Table 4 Grand daily means (with SEs in parentheses) of the mean deviation (MD) from individual lizards' *selected ranges* of the maximum and minimum operative temperatures, the field body temperatures of lizards (T_bs) and the estimated body temperatures of a randomly moving (thermoconforming) lizard (T_As).

	MD T_{max} (°C) (SE)	MD T_{min}° (°C) (SE)	MD field T_b (°C) (SE)	MD T_A (°C) (SE)
Summer	8.4 (1.3)	1.8 (0.4)	2.1 (0.5)	6.2 (1. 1)
Autumn	2.3 (0.3)	5.5 (0.4)	4.4 (0.5)	4.4 (0.7)

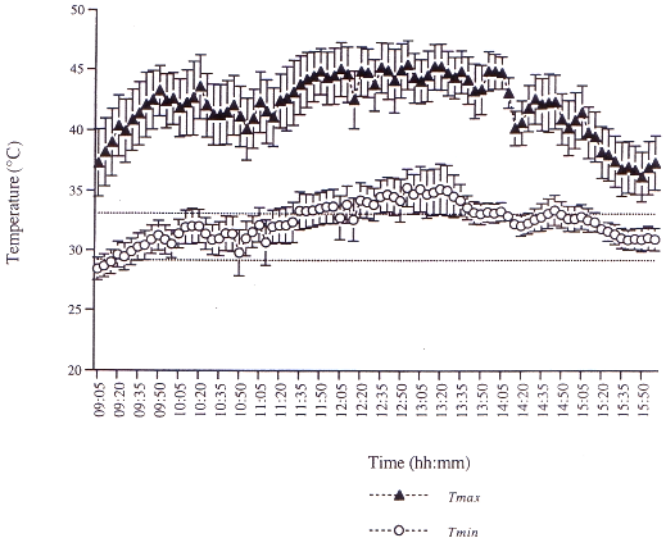

Fig. 3 Mean operative temperatures (with SEs) between 0905 and 1600 hours during summer. The two *horizontal lines* denote the upper and lower ends of the mean *selected range* for all study lizards

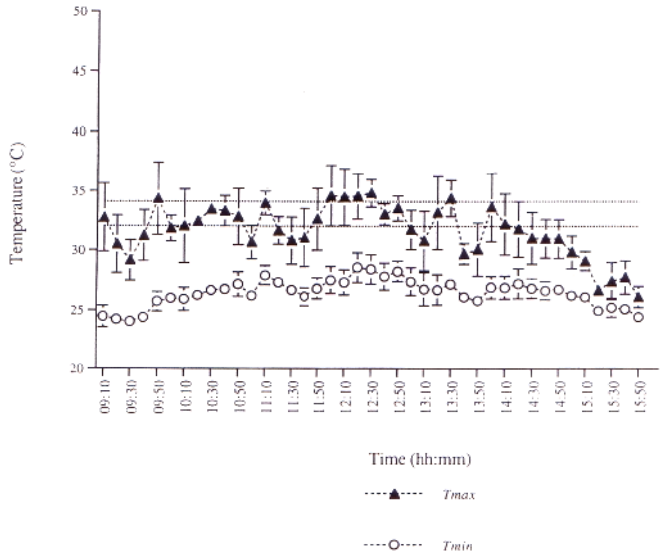

Fig. 4 Mean operative temperatures (with SEs) between 0905 and 1600 hours during autumn. The two *horizontal lines* denote the upper and lower ends of the mean *selected range* for all study lizards

Microhabitat choice

In summer, the study lizards did not select their thermal habitat on a random basis (Fig. 5). Comparisons of the mean proportion of time that the lizards spent in shaded. partially sunny, and sunny microhabitats, with those sampled by the random lizard, indicate that lizards avoided the full sun and favored the shade. These differences were statistically significant. In autumn, lizards experienced the thermal habitat on a more random basis (Fig. 6). There was no significant difference between the amount of time the observed lizards and the random lizard spent in fully shaded microhabitats. However, random lizards spent significantly more time in the full sun than the observed lizards. Changes in T_b over the day in summer and autumn lagged slightly behind increases and decreases in %sun (e.g. Fig. 7).

Data garnered through the use of the random lizard model indicate that the distribution of sun and shade on the ground differed between summer and autumn. The amount of shade present in the habitat increased and the availability of full sun decreased (Figs. 5 and 6). The sun's path is almost directly overhead in summer, but at a lower angle in autumn. There are also more daylight hours in summer than in autumn. For this reason we expect trees and bushes to throw longer shadows for a greater proportion of the observation period during autumn, so that a randomly moving lizard will experience the full sun less often in autumn than in summer.

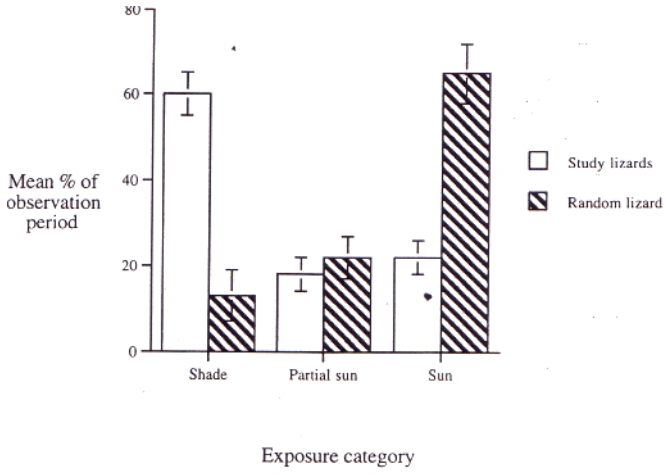

Fig. 5 The mean time per observation period (with SEs) that the study lizards and the random lizard spent in each sun exposure category during summer

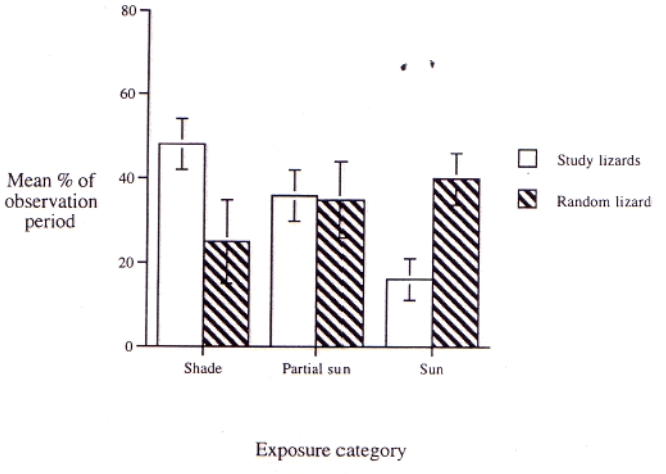

Fig. 6 The mean time per observation period (with SEs) that the study lizards and the random lizard spent in each sun exposure category during autumn

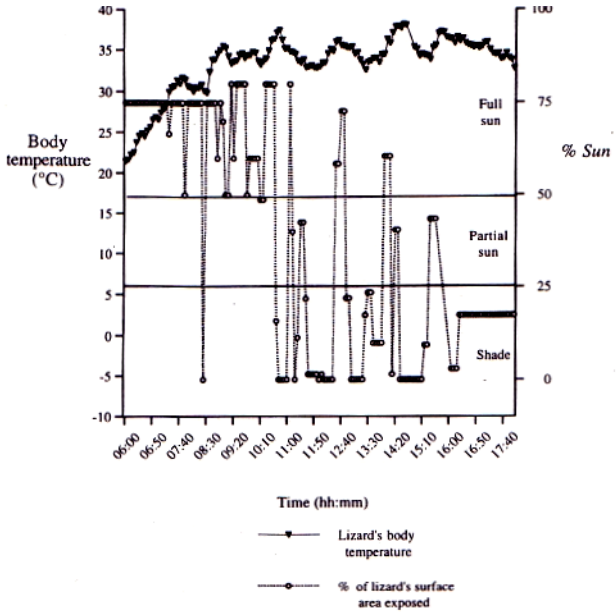

Fig. 7 The interaction between body temperature and sun exposure (*%sun*) for a single lizard over 1 day in summer

Body orientation

The expected proportions of orientations by a random lizard are 25% chest, 25% back, and 50% side. During summer the orientations back and side, which confer greater heat loads than chest (Muth 1977: Porter and James 1979; Stevenson 1985) were exhibited significantly less often by the study lizards than expected (Fig. 8). The proportion of the orientation chest did not differ significantly from random. It appears that the lizards were using body orientation adjustment to reduce heat load during summer. Conversely, in autumn the lizards appeared to be orientating randomly between 0905 and 1600 hours (Fig. 8). The only exception was the orientation chest, which was seen significantly less often than expected from a random lizard.

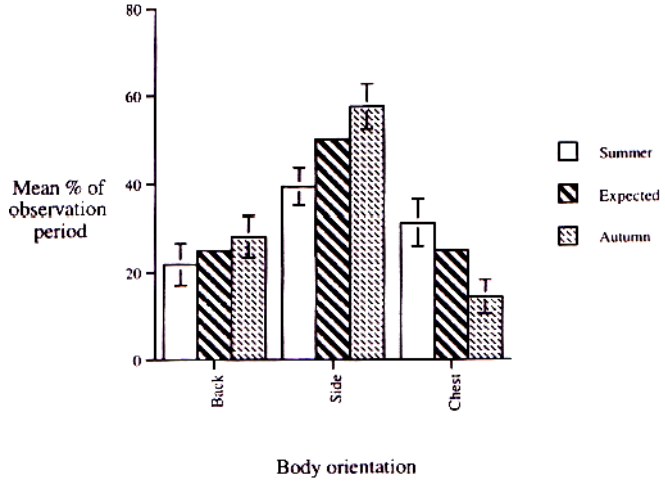

Fig. 8 The mean percent of the time per observation period (with SEs) that study lizards spent in each body orientation during summer and autumn, compared to that expected from a random lizard

Random lizard T_bs (T_As) and indices of thermoregulation

In summer, the lizard's mean daily field T_bs were significantly lower than those estimated for a thermoconforming lizard (T_AS) (Table 2). Indeed, during summer,

lizards experienced T_bs that were significantly closer to their own selected range than those of a random lizard (Table 4). We could not stabilize the sample variances for the mean daily field T_bs and T_AS recorded in autumn, but comparison of the mean T_b and T_A data for individual lizard-days suggests that any differences between the means are likely to have been small (authors, unpublished work, and see Table 2). Furthermore, the MDs of lizards' autumn field T_bs from the their selected ranges were not significantly different from those of the random lizard's (i.e., MD of field T_bs - MD of T_AS, Table 4).

Discussion

Deviation from the thermal trajectory of a randomly moving lizard (a thermoconformer) provides evidence for thermoregulation. During summer the study lizards behaved non-randomly with respect to two factors affecting heat load (%sun and body orientation). Conversely, our data suggest that they responded far less specifically to these factors during autumn. This in turn suggests that *P. barbata* thermoregulated in summer but not in autumn. Seasonal variation in thermoregulatory effort is also implied by comparisons of the daily means and central 50% ranges of field T_bs. These suggest that the lizards' summer field T_bs were significantly lower (~5°C) than those which a thermoconforming lizard would have experienced, yet the autumn T_bs for the two were quite similar (~2°C difference) (see Tables 2 and 3).

Combining behavioral data with T_b data provides additional evidence for a shift in thermoregulatory effort; the pattern seen in Fig. 7 clearly suggests that oscillations in T_b are a direct result of changes in %sun (see Bowker 1984). Indeed, *P. barbata* appear to have avoided allowing their T_bs to reach extremely high levels by "shuttling" in and out of the shade. The autumn data imply a similar situation. However, this type of relationship is valid evidence for the occurrence of shuttling as a behavioral mechanism for thermoregulation only if it can be shown that the lizards used sunny and shaded microhabitats nonrandomly. The lizards did this only during summer; and so such graphs provide evidence of thermoregulation for this season alone. The apparent linkage between fluctuations in %sun and field T_b in autumn is probably not due to any specific thermoregulatory behavior, and may simply reflect changes in the distribution of shade throughout the day. This is supported by observations that the lizards moved about very little in autumn (authors, unpublished work).

Based on purely physiological considerations. lizards might be expected to favor maintaining their T_bs within their selected ranges (Huey and Slatkin 1976; Christian and Bedford 1995), whether or not this requires active thermoregulation. Comparing the average mean deviation from the selected range (MD) of field T_bs with the average MD of a random lizard's T_bs is thus a convenient way of identifying thermoregulation. If the two types of MD are significantly different then the lizard, by definition, can be said to have thermoregulated.

During summer, the random lizard T_bs deviated from the selected range by about 4°C more (Table 4) than did *P. barbata* field T_bs - evidence for thermoregulation. However, during autumn the grand mean MDs for the lizards' T_bs were not significantly different from those for a random lizard. Here again we see a seasonal change in thermoregulatory effort. Christian and Weavers (1996) found seasonal changes in the extent of thermoregulation for several tropical varanids. Like *P. barbata* at our study sites, these varanids thermoregulated carefully in the summer wet (active) season but let their T_bs fall outside their selected ranges during periods of the year for which they were less active. These two examples suggest that facultative thermoregulation may be commoner than generally envisaged.

The overall average MD for a random lizard in summer was 6.2 ± 1.1°C, but only 2.1 ± 0.5°C for our study lizards. Not only are the two significantly different, but a MD of only 2.1 ± 0.5°C indicates that the lizards kept their T_bs close to their selected ranges during this time. The mean daily T_bs and operative temperatures for summer tell us that the T_bs of study and random lizards were generally above selected ranges, rather than below them (Table 2).

For a lizard, the difference between having a T_b 6°C above its selected range and one only 2°C above it is likely to have biological relevance. Elevated rates of evaporative water rates at high T_bs in *P. barbata* (then *Amphibolurus barbatus)* were documented by Warburg (1965). Indeed, Buttemer and Dawson (1993) observed a trebling of metabolic rate with a 10°C rise in T_b, (within the interval 25-42°C) in the marine iguana (*Amblyrhynchus cristatus).* Without thermoregulation in summer, *P. barbata* would have experienced T_bs close to the lethal limit (46°C: Warburg 1965) for much of the 0905-1600 hours observation period. Indeed, two lizards were observed gaping in the field in summer, when their T_bs were above 41°C. Danger of overheating in certain places or times of the day or year is

likely to be a common problem for lizards, e.g., *Dipsosaur˙us dorsalis* (DeWitt 1967), *Sauromalus obesus* (Zimmerman and Tracy 1989), and *Podarcis hispanica atrata* (Bauwens et al. 1996).

The results presented in this paper (although clearly subject to the limitations of small sample sizes and inadequacies inherent in the use of the copper models) suggest overwhelmingly that *Pogona barbata* thermoregulated in summer but probably did not do so in autumn. The behavioral data are especially important as they lend weight to the results gained through the use of the copper models, particularly considering the larger number of assumptions associated with the physiological data.

Having established that *P. barbata* do thermoregulate (at least for part of the year) and knowing that daytime field T_bs dropped around 7°C between summer and autumn, we are left with the question of which factors are likely to be responsible for the seasonal change in field T_b. Using the data gathered already we can address three main possibilities. First, there may be a seasonal change in the selected range (acclimatization). Second, the extent to which field T_bs are limited by the availability of operative temperatures might vary between seasons. Third, the costs and benefits of thermoregulatory behavior may vary between seasons and thus affect realized field T_bs.

A number of lizard species exhibit shifts in their selected range simultaneously with shifts in field T_bs (Christian and Bedford 1994; reviewed in Christian and Bedford 1995). However, in other species seasonal shifts in field T_bs can occur without changes in selected range (e.g., van Damme et al. 1987). *P. barbata* appears to fit the latter pattern, with mean *selected ranges* for the lizards in the present study not changing significantly between summer and autumn. Thus the observed reduction in field T_bs across seasons apparently cannot be explained by the hypothesis that a downwards shift in the range of T_bs which provide maximum physiological performance simply caused lizards to “select /prefer" lower T_bs in autumn.

The body temperatures of reptiles may be constrained by the thermal regimes of their environments during one or more seasons (Peterson 1987; van Damme et al. 1987; Grant 1990). Zimmerman and Tracy (1989) discovered that for some of each active season the physical availability of operative temperatures in the field constrained T_bs of the lizard *Sauromalus obesus* to those outside the selected range. However, for the most part, the range of operative temperatures available during the present study would not have prevented *P. barbata* from attaining T_bs within the selected range in either season had they chosen to do so.

Within a season, deviations of field T_bs from the selected range may represent the results of a trade-off between a lizard's physiological and ecological requirements. Changes in factors affecting these trade-offs could have been responsible for the variation in field T_bs between seasons, particularly changes in aspects of the lizards' social behavior and the spatial distribution of resources such as thermal microhabitats, territories and food supply. For example, Christian and Tracy (1985) noted that food source distribution and availability may play a role in determining the field T_bs of Galapagos iguanas. Additionally, Bauwens et al. (1996) have suggested that an apparently high abundance of food in certain microhabitats may have accounted for the presence of the lizard *Podarcis hispanica atrata* in those areas at thermally suboptimal times.

Although over by autumn (C. Schauble, personal observation), the annual breeding season was in full swing at the time of the summer sampling. Sunny, open areas were a focus for fervent social activity and foraging. DeWitt (1967) noted that male desert iguanas *(Dipsosarwus dorsalis)* sometimes allowed their T_bs to climb to extreme levels during territorial defense. Likewise, our study lizards also let their T_bs rise to high levels during social displays and foraging activity. Indeed, to avail themselves of operative temperatures within their selected range at midday during summer, the lizards would have needed to retreat high into the trees. Subsequent costs associated with resultant lapses in territory defense or missed mating opportunities could be high (Grant 1990). Presumably, in some situations the benefits associated with a particular behavior outweigh the detrimental effects of evaporative water loss, energetic outlay, and heat stress. No data on food distribution are available for our study sites.

The availability and distribution of microhabitats with differing thermal regimes are obviously important to a lizard's thermal ecology (Christian et al. 1986; Tracy and Christian 1986; Huey 1991). At our study sites, in both summer and autumn, sunny microhabitats were much more available than shaded ones (based on the random lizard's use of the two). Furthermore, shady areas tended to be separated by large tracts of sunny habitat. These sunny areas posed heat stress problems for *P. barbata* during summer (see above) but not in autumn. The mean T_{max} was much lower in autumn than it had been in summer, down from 42.1 ± 1.7°C to 31.7 ± 1.2°C. The T_bs of both the study and random lizards were below the selected range in autumn, but the mean T_{min} was not low enough to represent a serious cold stress threat (see the discussion of *P. barbata's* metabolic scope for activity in Bartholomew and Tucker 1963).

During autumn we did not see any lizards descend from their trees (unlike in summer), even though the copper models showed that ground-level microhabitats could have provided T_bs within the selected range. If we had placed our models in the trees, it is likely that subsequent T_AS would have been slightly lower than those estimated from models on the ground (due to, e.g., increased air flow, Stevenson 1985). However, behavioral observations suggest that the lizards chose thermal microhabitats and orientated reasonably randomly in autumn. Therefore it seems unlikely that there was an active and thermally triggered bias towards microhabitats conferring low T_bs. Lizards probably avoided ground-level microhabitats during autumn for other reasons. such as the higher predation risk and the extra energy expenditure associated with climbing to and from them. Note though, that Porter and James (1979) calculated that being in the shade reduced the daily energy requirement of *Agama agama* by 11-19%. This may be an advantage in autumn, if food supply is reduced at this time.

Huey and Slatkin (1976) predicted that thermoregulatory accuracy should increase if the productivity of the habitat increases. It seems that to take advantage of the high "productivity" of the summer breeding season lizards are forced to spend short periods of time at physiologically undesirable temperatures. Maybe *P. barbata* reduce the physiological costs incurred in summer by thermoregulating accurately whenever possible and, when not possible, acting quickly to regain less stressful T_bs after excursions. We also suggest that accurate thermoregulation may not have occurred during autumn because the low likelihood of thermal stress made it an extravagance.

Acknowledgements We thank Culum Brown and Robbie Wilson for their generous contributions of time towards field work and discussions. Special appreciation also to Keith Christian and Gavin Bedford for supplying unpublished manuscripts and to Data Electronics Pty. Ltd. for their supply of equipment. Last, but not least, we wish to thank Joan Whittier and family, Heidi Robertson. Lyn Beard, Kevin Warburton, Robyn Rolfe and David Yates for assorted forms of assistance. This work was approved by the University of Queensland Animal Experimentation Ethics Committee and conducted with appropriate permits from the Queensland Department of Environment and Heritage. Our study was supported by a University Research Grant from the Zoology Department, The University of Queensland.

References

Adolf SC (1990) Influence of behavioural thermoregulation on microhabitat use by two *Sceloporus lizards.* Ecology 71:315-327

Bakken GS (1992) Measurement and application of operative and standard temperatures in ecology. Am Zool 32:194-216

Bartholomew G (1982) Physiological control of body temperature. In: Gans C, Pough FH (eds) Biology of the Reptilia, vol 12. Physiology C. Physiological ecology. Academic Press, New York, pp 167--211

Bartholomew GA, Tucker VA (1963) Control of changes in body temperature metabolism, and circulation in the agamid lizard. *Amphibolurus barbatus.* Physiol Zool 36:199-218

Bauwens D, Hertz PE, Castilla AM (1996) Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. Ecology 77:1818-1830

Bowker RG (1984) Precision of thermoregulation of some African lizards. Physiol Zool 57:401--412

Brattstrom 13H (1971) Social and thermoregulatory behavior of the bearded dragon *Amphibolurus barbatus.* Copeia 1971:484-497

Buttemer WA, Dawson WR (1993) Temporal pattern of foraging and microhabitat use by Galapagos marine iguanas, *Amblyr-ynchus cristatis* Oecologia 96:56-64

Christian K, Bedford G (1994) Thermoregulation by the spotted tree monitor, *Varanus scalaris,* in the seasonal tropics of Australia. .I Therm Biol 21:67--73

Christian KA, Bedford GS (1995) Seasonal changes in thermoregulation by the frillneck lizard, *Chlamydosaurus kingii,* in tropical Australia. Ecology 76:124-132

Christian KA, Tracy CR (1985) The physical and biotic determinant of space utilization by the Galapagos land iguana. Oecologia 66:132-140

Christian KA, Weavers BW (1996) Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. Ecol Monogr 66:139-157

Christian KA, Tracy CR, Porter WP (1983) Seasonal shifts in body temperatures and use of microhabitats by Galapagos land iguanas *(Cononphus pallidus).* Ecology 64:463--168

Christian KA, Clavijo IE, Cordero-Lopez N, Ellias-Maldonado EE, Franco MA, Lugo-Ramirez MV. Marengo M (1986) Thermoregulation and energetics of a population of Cuban Iguanas *(Cyclura nubila)* on Isla Magueyes, Puerto Rico. Copeia 1986:65-69

Cogger HG (1992) Reptiles and amphibians of Australia. Reed. Sydney

Crawford EC Jr (1980) Behavioural aud autonomic thermoregu-lation interrestrial ectotherms. In: Richard Taylor C, Johansen K, Bolis L (eds) A companion to animal physiology. Cambridge University Press, Cambridge, pp 198--215

Damme R van, Bauwens D, Verheyen RF (1987) Thermoregulatory responses to environmental seasonality by the lizard Lacerta vivipara. Herpetologica 43:405-415

Damme R van, Bauwens D, Castilla AM, Verheyen RF (1989) Altitudinal variation of the thermal biology and running performance in the lizard Podarcis tiliguerta. Oecologia 80:516-524

DeWitt CB (1967) Precision of thermoregulation and its relation to the environmental factors in the desert iguana Dipsosaurus dorsalis Physiol Zool 40:49-66

Diaz JA (1992) Choice of compass directions around shrub patches by the heliothermic lizard Psammodromus algirus. Herpetologica 48:293-300

Diaz JA (1994) Field thermoregulatory behavior in the western Canarian lizard Gallotia galloti. J Herpetol 28:325-333

Ellner LR, Karasov WH (1993) Latitudinal variation in the thermal biology of ornate box turtles. Copeia 1993:447-455

Garrick LD (1974) Reproductive influences on behavioral thermoregulation in the lizard, Sceloporus cyanogenys. Physiol Behav 12:85-91

Garrick LD (1979) Lizard thermoregulation: operant responses for heat at different thermal intensities. Copeia 1979:258-266

Grant BW (1990) Trade-offs in activity time and physiological performance for thermoregulating desert lizards, Sceloporus merriami Ecology 71:2323-2333

Griffiths K (1987) Reptiles of the Sydney region. Three Sisters, Winmalee

Grigg G, Augee ML, Beard LA (1992) Thermal relations of free living echidnas during activity and in hibernation in a cold climate. In: Augee ML (ed) Platypus and Echidna. Royal Zoological Society of New South Wales, Sydney pp 160-173

Heatwole H, Taylor J (1987) Ecology of reptiles. Surrey Beatty, Chipping Norton

Hertz PE (1974) Thermal passivity of a tropical forest lizard *Anolis polylepis*. J Herpetol 8:323-327

Hertz PE (1992) Evaluating thermal resource partitioning by sympatric lizards *Anolis cooki* and *A. cristatellus*: a field test using null hypotheses. Oecologia 90:127-13G

Hertz PE, Huey RB, Stevenson RD (1993) Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. Am Nat 142:796-818

Huey RB (1974) Behavioral thermoregulation in lizards: importance of associated costs. Science 184:1001-1003

Huey RB (1982) Temperature, physiology and the ecology of reptiles. In: Gans C, Pough FH (eds) Biology of the Reptilia vol 12. Physiology C. Physiological ecology. Academic Press, New York, pp 2G-90

Huey RB (1991) Physiological consequences of habitat selection. Am Nat 137:S91-SI IS

Huey RB, Slatkin M (1976) Cost and benefit of lizard thermoregulation. Q Rev Biol 51:3G3-384

Huey RB, Webster TP (1976) Thermal biology of Agolis lizards in a complex fauna: the cristatellus group on Puerto Rico. Ecology 57:985-994

Kingsbury BA (1994) Thermal constraints and eurythermy in the lizard *Elgaria multicarinata* Herpetologica 50:266-273

Lee AK, Badham JA (1963) Body temperature, activity and behavior of the agamid lizard, *Amphibolurus barbatus*. Copeia 1963:387-394

Licht P, Dawson WR, Shoemaker VH, Main AR (1966) Observations on thermal relations of West Australian lizards. Copeia 1966:97-110

Manning B, Grigg GC (1997) Basking is not of thermoregulatory significance in the "basking" freshwater turtle *Emydura signata*. Copeia 1997: pp 579-584

Muth A (1977) Thermoregulatory postures and orientation to the sun: a mechanistic evaluation for the zebra-tailed lizard, *Callisaurars draconoides*. Copeia 1977:710-720

Peterson CR (1987) Daily variation in the body temperatures of free ranging garter snakes. Ecology G8:160-169

Porter WP, James FC (1979) Behaviour and microclimate relationships in the African rainbow lizard *Agama agama*. Copeia 1979:585-593

Seebacher F (1993) Thermal relations of *Crocodylus johnstoni* (Krefft 1873) in the wild. PhD thesis, University of Queensland Shine R (1980) "Costs" of reproduction in reptiles. Oecologia 46:92-100

Shine R, Lambeck R (1990) Seasonal shifts in the thermoregulatory behaviour of Australian blacksnakes, *Pseudechis porphyriacus* (Serpentines: Elapidae). J Therm Biol 15:301-305

Slip DJ, Shine R (1988) Thermophilic responses to feeding of the diamond python, *Morelia s. spilota* (Serpentines:Boidae). Comp Biochem Physiol 89A:G45-G50

Stevenson RD (1985) The relative importance of behavioural and physiological adjustments controlling body temperature in terrestrial ectotherms. Am Nat 126:362-386

Stevenson RD, Peterson CR, Tsuji JS (1985) The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. Physiol Zool 58:4G--57

Tracy CR, Christian KA (1986) Ecological relations among space, time, and thermal niche axes. Ecology 67:609-G15

Warburg MR (1965) The influence of ambient temperature and humidity on the body temperature and water loss from two Australian lizards *Tiliqua rugosa* and *Amphibolurus barbatus*. Aust J Zool 13:331-350

Zimmerman LD, Tracy CR (1989) Interactions between the environment and ectothermy and herbivory in reptiles. Physiol Zool 62:374-409